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Win, lose or draw: a comparison of fight structure based on fight conclusion in the fallow deer

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Summary

Fights between male fallow deer (*Dama dama*) may conclude with the contest decisively resolved in favour of one animal (the winner), or, there may be an inconclusive resolution, in which case there is no winner. We sought to compare the structure of fights between male fallow deer in order to determine what factors might be important in influencing how fights are concluded (i.e., decisively or inconclusively resolved). We compared differences in the number of backward pushes, jump clashes and retreats over fight duration; we also compared the duration of bouts of fighting. Fights that were decisively resolved had a significantly higher number of backward pushes and jump clashes than fights that were inconclusive. Decisively resolved fights also had a higher number of retreats in the final quarter of contests suggesting that, overall, fights that resulted in a winner were more costly than fights that were inconclusively resolved. There was a significantly larger asymmetry between opponents in decisively resolved fights in the proportion of backward pushes and jump clashes recorded suggesting that opponents in fights that ended inconclusively were more evenly matched. There was no difference in overall contest duration or the duration spent fighting between decisively and inconclusively resolved fights. These results indicate that the manner by which a contest concludes, is determined by the difference in action performance between contestants and also, a difference in the rate of behavioural actions as a function of time spent fighting.

Keywords: fight structure, fight conclusion, assessment process, fallow deer.

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Introduction

Recent empirical and theoretical work in the field of animal competition has focussed on description and quantification of contest behaviour. Empirical data are frequently used in an attempt to understand the underlying assessment processes that operate during contests between members of the same population (Enquist & Leimar, 1983; Enquist et al., 1990; Mesterton-Gibbons et al., 1996; Payne & Pagel, 1996, 1997; Payne, 1998; Taylor & Elwood, 2003). A common approach is to compare dyadic interactions during contests in relation to such factors as resource ownership and availability, physiological state, prior experience and asymmetries in RHP-related factors such as body size and /or weapon size (see Huntingford & Turner, 1987; Archer, 1988; Riechert, 1998 for reviews). This has resulted in a considerable number of experimental studies in which opponents are systematically matched in staged encounters, thereby increasing the probability that a contest and a decisive outcome will occur (e.g., Hack, 1997; Neat el al., 1998; Briffa & Elwood, 2000; Hsu & Wolf, 2001). Conversely, interactions recorded during field studies, where experimental control is generally absent, suffer from the drawback that factors such as the identity of the competitors, physiological state and asymmetries in RHP are often unknown. This has the effect of making performance within and between temporally extended contests difficult to determine.

Contestant behaviour during escalated contests frequently involves the repetition of specific behavioural actions (Payne & Pagel, 1997; Payne, 1998). The rate at which these displays occur can be variable; for instance, signal rate between opponents may be matched (e.g., Jakobsson et al., 1979; Glass & Huntingford, 1988; Marden & Waage, 1990; Smith et al., 1994; DiMarco & Hanlon, 1997) or unmatched (e.g., Turner & Huntingford, 1986; Franck & Ribowski, 1989; Enquist et al., 1990; Popp et al., 1990; Turner, 1994; Briffa et al., 1998; Neat et al., 1998). The relationship between contestant behaviour and contest outcome has been incorporated into game theoretical models of aggressive behaviour. Models such as the sequential assessment model (SAM: Enquist & Leimar, 1983; Leimar & Enquist, 1984; Enquist et al., 1990) and the energetic war of attrition (eWOA: Mesterton-Gibbons et al., 1996; Payne & Pagel, 1996, 1997), predict that decision rules are indicated by the display rate of individual contestants. It is through monitoring these display rates, that assessment rules used by competing animals

may be determined (Taylor & Elwood, 2003). The majority of studies published to date have used data generated from laboratory experiments both in model development and as support for particular theoretical models. Given that experimental studies, in general, result in contests that are decisively resolved, the predictions and development of these models are generally silent when the contest terminates with an inconclusive outcome.

The present study seeks to investigate differences in fight structure between contests that are decisively resolved and those that are not, using the European fallow deer as the model species. Modelling the structure of contests between mature fallow deer is complex (Jennings et al., 2004, in press). However, based on our current understanding of contest structure within this species, fighting between fallow deer satisfies some of the predictions of the energetic war of attrition (Jennings et al., 2004). Fighting between males is concentrated just prior to and during the annual rutting period during October in the Northern hemisphere as males compete for access to oestrus or peri-oestrus females (Moore et al., 1995). Fights consist of repeated bouts of fighting that are separated by pauses of varying duration, during bouts of fighting the antlers of both protagonists are locked and a vigorous pushing contest ensues (Alvarez, 1993; Jennings et al., 2002, in press). In decisively resolved fights, these bouts of fighting continue until one animal quits the contest by running or walking away, often pursued by the victor. However, many fights terminate inconclusively and typically, the contestants gradually move away from each other such that there is no obvious winner. A previous study (Jennings et al., 2004), indicated that RHP-related factors such as larger body mass and longer antlers did not confer competitive advantages on the bearer during fights, nor did the larger opponent engage in higher levels of aggressive behaviour during fights. Therefore, the rate of behavioural actions within and between contests may be important in determining how a fight is concluded. Our goal in the present study is to undertake an investigation of fight structure by focussing on the behavioural actions of contestants based on fight conclusion.

Methods

Study site and population

This study was conducted in 1996 and 1997 on a herd of free-ranging European fallow deer in Phoenix Park, Dublin, Ireland (53°22′N, 6°21′W). The

park encloses 709 hectares of which approximately 80% is available to the deer. At the beginning of November 1996 there were 152 fawns, 394 females ($\geqslant$1 year old) and 172 males ($\geqslant$1 year old) in the herd. At the beginning of November 1997 there were 172 fawns, 349 females ($\geqslant$1 year old) and 197 males ($\geqslant$1 year old). Most males were tagged (1996: 97%; 1997: 93% $\geqslant$ four years old) and all could be individually recognised by antler shape and coat colour.

Procedures

The herd was observed from late August and fights were recorded on videotape during October in 1996 and 1997. All agonistic interactions were recorded using all-event recording procedures (Altmann, 1974); data recorded included the identities of the two animals involved in the interaction, and the time, date and location of the interaction. Video taped fight sequences were analysed using the Observer Video Tape Analysis System (Noldus Information Technology, Wageningen, The Netherlands). Although fights were recorded before the rut began we considered the presence of the oestrus female a resource over which males fought, and there was a positive relation between the numbers of matings recorded and fights (1996: $r_s = 0.77$, $N = 16$, $p < 0.001$; 1997: $r_s = 0.66$, $N = 17$, $p < 0.004$). While there is a positive relation between resource abundance and fight frequency, it is unlikely to have influenced fight conclusion; a similar proportion of fights were recorded as inconclusively resolved in the pre-rut when there were no receptive females in the herd (1996: 54.4%; 1997: 56.2%) as were recorded in the rut (1996: 51%; 1997: 58.5%).

Some males adopted transient territories in an oak wood at the periphery of the female's daytime range, but in general they tended to move off their territories and follow the females after they moved through the wood early in the morning and onto their day range that consisted of open pasture (Moore et al., 1995). Here males interacted both with other males where fights frequently occurred, and engaged in rutting behaviour such as herding females, scent marking, vocalizing and wallowing (Chapman & Chapman, 1975). The choice of mating tactic adopted by individual male fallow deer varies considerably (Langbein & Thirgood, 1989) and might influence not only the rate at which fighting is engaged in, but also other related factors, such as fight duration (Pélabon et al., 1999). The majority of matings and fights recorded in

Phoenix Park occur off individual males' territories (Moore et al., 1995), and it is these fights that are the focus of the present study. By using only non-territorial contests, the present study sought to avoid potential confounding factors such as, fights between neighboring males over territorial boundaries or fights due to territorial intrusions.

Fighting with other males is costly not just in energetic terms because it leads directly to a loss of any females currently being herded and, therefore, fighting contributes directly to the loss of the resource irrespective of how a fight concludes. There were 189 fights recorded on videotape between different males and these were classified as either concluding decisively (winner and loser) or inconclusive (no winner) based on the behaviour of males following the end of the interaction. We recorded 98 fights (51.9%) where there was a clear winner and loser. The behaviour of winners and losers immediately following fighting was particularly obvious; losers tended to run away from their opponent often pursued for a variable duration and distance by the winner. Where a fight was inconclusively resolved, both animals moved slowly away from each other. This was particularly obvious when fights ended with a parallel walk; both bucks separate from the parallel walk by moving gradually in opposite directions (Jennings et al., 2003).

Typically the terms, *fight outcome* and *fight result*, have been used to define the two contestants in a dyadic encounter, i.e., the winner and the loser. Therefore, in the present study we adopt the term *fight conclusion* to indicate the status of the fight at the end of the interaction (decisively resolved (or won) and not decisively resolved (or inconclusive)). We measured the total fight duration in seconds as the time from first antler contact to last antler contact (Clutton-Brock & Albon, 1979). The backward push and jump clash involve direct physical contact between contestants and these were selected from fight sequences for detailed analysis. The backward push and jump clash have been described elsewhere (Alvarez, 1993; Jennings et al., 2004). The retreat, another obvious behaviour during fights was analysed in detail. During a retreat one animal backed slowly away from his opponent with antlers lowered such that antler contact was broken; his opponent often raised his antlers and slowly followed the retreating male. A retreat could end with either the retreating male turning rapidly away from his opponent and running away (see also Clutton-Brock et al., 1982) or his opponent could re-initiate antler contact and continue the fight.

We divided fights in quarters based on fight duration and the number of backward pushes, jump clashes and retreats per fights quarter was calculated. Given that fight duration was variable (Jennings et al., 2004), the number of backward pushes, jump clashes and retreats (N_t) during each fight quarter (Q_t) was expressed as responses per minute, calculated as $60^* N_t/Q_t$. Where a backward push, jump clash or retreat was not recorded during a fight, it was eliminated from that analysis and hence df vary. Furthermore, we set a minimum criterion of 10 s for fight duration and this removed seven fights that resulted in a winner and fourteen fights that ended inconclusively from the analysis of behavior over fight quarter. Fallow deer fight by repeatedly locking their antlers in bouts of fighting separated by pauses during which antler contact is broken. In order to determine whether there were changes in bout structure as bucks fought, we calculated both the duration of the first four bouts of fighting and the duration of the backward push within those bouts in seconds (Briffa & Elwood, 2000). Because not all fights had four bouts of fighting before they ended the sample of fights in each category was reduced; 51 (52%) of fights that concluded with a winner and 47 (51.6%) fights that were inconclusive. Statistical analyses were performed using SPSS for Windows and simple main effects were computed using Esperstat for Macintosh. All p values are two-tailed.

Results

Fight duration

A comparison of overall fight duration from all fights recorded on videotape and based on fight conclusion indicated that duration was similar whether the fight was won ($\bar{x} = 88.12 \pm 8.4$ s) or inconclusive ($\bar{x} = 106.88 \pm 8.4$ s; Mann-Whitney U-test: $z = -0.27$, $N_1 = 98$, $N_2 = 91$, NS). When only the duration of bouts of fighting (i.e., when the contestants were in antler contact) was compared, fights that were won ($\bar{x} = 50.44 \pm 5.4$ s) were of similar duration to fights that were inconclusive ($\bar{x} = 45.2 \pm 6.3$ s; log transformed t-test: $t_{187} = 0.11$, $N_1 = 98$, $N_2 = 91$, NS).

Distribution of the backward push over fight quarter

From the sample of fights based on outcome, 8 (8.8%) that were won and 16 (20.7%) that were drawn had no backward push and so were eliminated from

Table 1. A comparison of the rate of the backward push, jump clash and retreat per minute over fight quarter and between fights that were decisively resolved or inconclusive.

	Backward Push	Jump Clash	Retreat
Fight Quarter	$F_{3,405} = 6.58$, $p < 0.001$	$F_{3,282} = 1.35$ NS	$F_{3,345} = 4.14$, $p < 0.007$
Conclusion	$F_{1,135} = 6.01$, $p < 0.01$	$F_{1,94} = 9.17$, $p < 0.003$	$F_{1,94} = 3.44$, $p = 0.066$
Interaction	$F_{3,405} = 1.78$ NS	$F_{3,282} = 0.19$ NS	$F_{3,345} = 2.67$, $p < 0.048$
Fight Won	–	–	$F_{3,345} = 8.58$, $p < 0.001$
Fight Inconclusive	–	–	$F_{3,345} = 1.01$ NS

the analysis. The difference between contestants in the percentage of backward pushes achieved was greater for fights that were decisively resolved (76.5% in favour of winner) than it was for fights that were inconclusive (59.8% in favour of one animal). Therefore, in fights that were inconclusive, the asymmetry in the proportion of backward pushes between contestants was closer to 50% than it was for fights that were won and the difference was significant (Independent t-test arsine transformed: $t_{142} = 2.73$, $p < 0.007$). The distribution of the backward push over fight quarter was expressed as the average between the two opponents and computed as actions per minute. Repeated measures ANOVA investigated the distribution of the backward push over fight quarter and fight conclusion (win/inconclusive). There was a significant decline in the number of backward pushes per minute recorded over fight quarter (Table 1 and Figure 1). There was also a main effect of fight conclusion with fights that had a decisive conclusion having significantly more backward pushes per minute than inconclusive fights. There was no interaction between fight quarter and outcome (Table 1).

The majority of fights that were decisively resolved had at least one backward push in the first four bouts of fighting (49/51, 96.1%); this figure was somewhat lower for fights that were inconclusive (34/47, 72.3%). When expressed as a percentage of the duration spent in backward push during the first four bouts of fighting, the duration spent in backward push was longer for fights that were decisively resolved (19.3%) than for fights that were inconclusive (13.9%; Independent t-test arsine transformed: $t_{81} = 2.23$, $p < 0.02$).

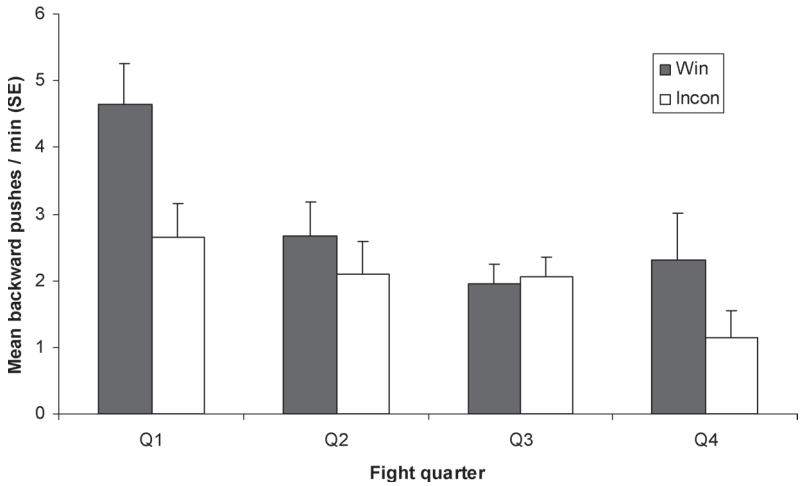

Figure 1. The average number of backward pushes per minute that were recorded over fight quarter based on fight conclusion.

The average duration of bouts that had a backward push and those that did not, were compared within fights. We therefore removed any fights that did not have a backward push in the first four bouts of fighting (Won fights: $N = 2$; Inconclusive fights: $N = 15$) and fights that had a backward push in all four bouts of fighting (Win: $N = 4$; Incon: $N = 0$). ANOVA (log transformed) was used to compare average bout duration based on fight conclusion (won versus incon) and presence/absence of a backward push. Bouts of fighting where there was a backward push were longer than bouts that did not have a backward push ($F_{1,76} = 113.36$, $p < 0.001$). There was no main effect of fight conclusion ($F_{1,76} = 0.01$, NS) and no interaction ($F_{1,76} = 0.003$, NS). When the duration of the backward push was removed from the overall bout duration a similar result was observed. Bouts of fighting with a backward push were longer than bouts that had no backward push ($F_{1,76} = 55.26$, $p < 0.001$). There was no main effect of fight conclusion ($F_{1,76} = 0.09$, NS) and there was no interaction ($F_{1,76} = 0.07$, NS).

Distribution of the jump clash over fight quarter

In total, there were 39 fights (42.9%) that were won and 33 fights (42.8%) that were inconclusive that did not have a jump clash recorded. These fights were removed from further analysis. A comparison of the percentage differ-

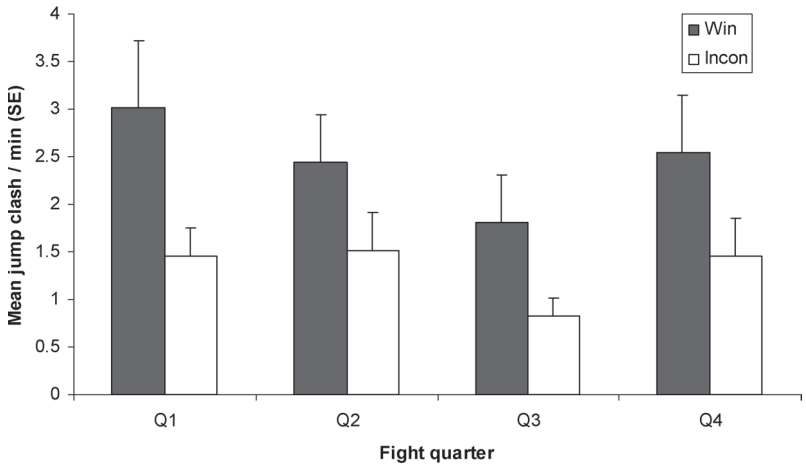

Figure 2. The average number of jump clashes per minute that were recorded over fight quarter based on fight conclusion.

ence in the number of jump clashes given by either of member of the dyad indicated that when fights were won, 86.2% of jump clashes were given by one member of the dyad (the eventual winner) compared with 61.1% during fights that were inconclusive. The difference in the proportion of jump clashes given between opponents was significant (Independent t-test arsine transformed: $t_{94} = 3.39$, $p < 0.001$). Repeated measures ANOVA indicated that the number of jump clashes did not differ over fight quarter and there was no fight quarter by fight conclusion interaction (Table 1 and Figure 2). However, there was a difference based on fight conclusion with fights that resulted in a clear winner having significantly more jump clashes per fight quarter than fights that were inconclusive (Table 1).

Distribution of the retreat over fight quarter

There were 11 (12.1%) fights that were won and 40 (51.9%) fights that were inconclusive that did not have a retreat recorded and they were removed from the analysis. The proportional difference in the number of retreats given by one member of the dyad was similar irrespective of conclusion with 97.4% of retreats initiated by the loser if the fight was won, and 95.2% of retreats by one contestant if the fight was inconclusive (Independent t-test arsine transformed: $t_{115} = 0.76$, NS). Repeated measures ANOVA was used to compare the average number of retreats per minute over fight quarter. There was a

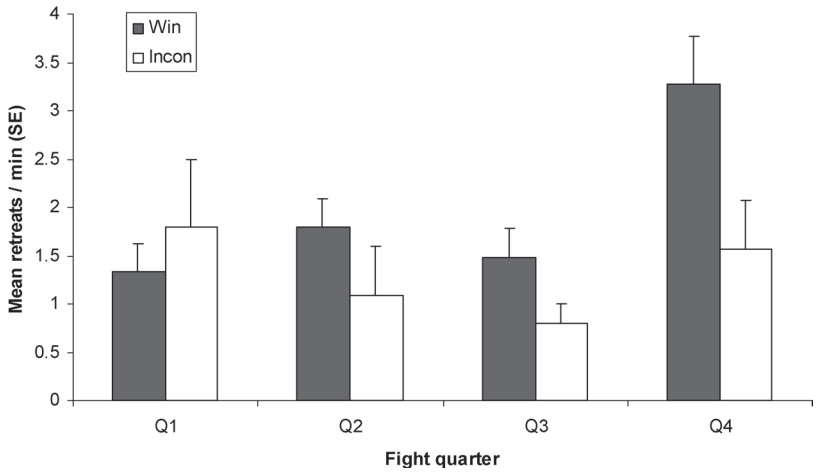

Figure 3. The average number of retreats per minute that were recorded over fight quarter based on fight conclusion.

significant increase in the number of retreats as a function of fight quarter (Table 1 and Figure 3). There was no difference in the number of retreats recorded based on fight conclusion although it did approach significance and there was a significant fight quarter by fight conclusion interaction. Based on the significant interaction we computed simple main effects to determine the source of the interaction. There was a significant difference in the number of retreats recorded over fight quarter when fights resulted in a winner but not when the fight was inconclusive (Table 1). The source of the difference in fights that were won was as a result of the high number of retreats recorded in the last quarter of fights ($F_{1,460} = 8.43$, $p < 0.004$).

Discussion

A fight is an interaction between two opponents that seek to defeat each other (López & Martín, 2001), and as a consequence empirical and theoretical studies have tended to focus on winner-loser behaviour during contests. Therefore, little attention has been paid to fights that are not decisively resolved although some authors concede that inconclusive results may be possible (e.g., Hamilton & McNutt, 1997) and inconclusive results have been noted in other studies (e.g., Festa-Bianchet et al., 1990; Neat et al., 1998). The goal of the present study was to investigate contest structure with regard

to how fights between male fallow deer concluded. This was prompted by the observation that a substantial number of fights (approximately 50%) which were recorded, were not decisively resolved in favour of one contestant. Previous research has indicated that RHP correlated factors such as larger body weight and longer antlers do not confer competitive advantages to the larger individual (Jennings et al., 2004). We therefore, compared behavioural rates between fights that were won and fights that were inconclusive to investigate whether this factor was important.

Game theoretical models such as the SAM (Enquist & Leimar, 1983; Enquist et al., 1990) and the eWOA (Mesterton-Gibbons et al., 1996) predict that display rate of opponents is a central feature in determining the assessment rules used between competing animals (Taylor & Elwood, 2003). Under the SAM, contests are predicted to move through distinct phases of increasing intensity. If two animals are unable to resolve a contest by low-level display behaviour they escalate through more intense phases until one animal determines it cannot win and yields. A critical element in the assessment process is that escalation to more intense phases of the contest only occurs because neither animal can assess a difference between their opponents quality relative to their own based on a comparison of their display rates (Enquist et al., 1990). The observation that over half of the fights we observed end inconclusively might be explained within a theoretical framework such as SAM. In decisively resolved fights there were differences between winners and losers in the number of backward pushes and jump clashes recorded, with winners achieving more backward pushes and jump clashes than losers (Jennings et al., in press; this study). However, in fights that were inconclusive, the asymmetry between opponents in the proportion of both the backward push and the jump clash given was significantly smaller than in fights that were won. The SAM expects a certain level of error in opponent assessment and predicts that large differences between opponents are easier to detect than small differences (Enquist & Leimar, 1983). The present results concerning the backward push and jump clash might be interpreted such that neither contestant in an inconclusive fight was able to accurately assess a difference in the quality of their opponent relative to their own abilities, consistent with the SAM. However, our results also show that there are significantly fewer backward pushes and jump clashes during inconclusive fights than during fights that concluded with a winner. Furthermore, fight duration and duration spent fighting were similar irrespective of fight conclusion.

Where opponents monitor each other's display rate we would expect that that there should be more backward pushes and jump clashes in fights that are inconclusive and, that fights should be longer as opponents attempt to assess differences in individual quality. This was not the case and, therefore, we conclude that opponent assessment is unlikely to be a mediating factor in determining how fights conclude.

Division of fights into quarters based on contest duration has commonly been employed to investigate temporal changes in behaviour over the course of an interaction (e.g., Dow et al., 1976; Jakobsson et al., 1979; Turner & Huntingford, 1986; Smith et al., 1994; Huntingford et al., 2000). An analysis of the temporal aspects of fight structure indicated that there were changes in the frequency of the backward push over fight quarter. In the case of the backward push, the majority of these actions were given in the first quarter during fights that were won while in inconclusive fights backward pushes were evenly distributed over fight quarter. Where a fight was decisively resolved, bout duration over successive bouts of fighting declined; this was not observed for fights that were inconclusive. We have shown that the backward push was more likely to occur in longer bouts of fighting than in shorter bouts indicating some cost threshold must be passed before one contestant is displaced in a backward push. The significant reduction in the number of backward pushes recorded over fight duration in decisively resolved contests is likely to be a result of this threshold not being reached due to successively shorter bouts of fighting (Jennings et al., in press).

It is a consistent finding that the rate at which signals are emitted during contests can influence the outcome of a fight (e.g., Clutton-Brock et al., 1979; Rivero et al., 2000; Briffa et al., 2003). Furthermore, the frequency or vigour with which animals repeat use of a particular behaviour might represent the motivational level of individual competitors (e.g., Hack, 1997; Briffa et al., 1998). The energetic cost of the backward push is expected to be higher for the animal that displaces his opponent (Jennings et al., 2004). In addition, the jump clash is regarded as a high-risk high-cost behaviour in terms of the potential for both physical injury and antler breakage (Alvarez, 1993). The pattern of results recorded for the backward push and the jump clash was similar based on fight conclusion. There were more backward pushes and jump clashes recorded during fights that concluded decisively than in inconclusive fights. Furthermore, decisively resolved fights had proportionally longer duration of backward pushes than inconclusive fights. We recorded a

higher proportion of both backward pushes and jump clashes given by one contestant (the winner) in fights that were decisively resolved than in inconclusive fights. Therefore, the rate at which individual contestants engage in fighting (e.g., jump clash) is an important determinant of fight conclusion, a finding that is consistent with previous studies that have addressed signal rate during contests. Within a theoretical framework such as that proposed by Payne & Pagel (1996) the effects of fighting are expected to differ between opponents based on the ability to inflict costs on the one hand and to incur costs on the other. Superior competitors (winners) are expected to inflict higher costs on their opponents, leading to a faster accrual of costs for the weaker contestant (loser; Payne & Pagel, 1996). Given that there is a difference in the rate of both the backward push and jump clash between fights based on conclusion, and, differences between competitors within fights in the rates of action, we suggest that an important factor in determining how a fight concludes is related to rate at which competitors both inflict and incur fight related costs.

Although fight duration did not differ based on fight conclusion there were significantly higher numbers of backward pushes and jump clashes recorded during fights that were won, compared with inconclusive fights. This indicates that the overall rate of actions (backward push or jump clash) per unit time rather than amount of time spent fighting per se is the crucial parameter in determining how a fight might conclude (Payne & Pagel, 1997). Under the framework of Payne & Pagel (1996) the ability to absorb the costs of fighting decreases over contest duration. Therefore, time associated costs of performing either a backward push or jump clash are cumulative and can accrue in a sub-linear fashion resulting in a decline (or de-escalation) in behavioural acts as a function of time spent fighting (Payne & Pagel, 1996, 1997). The significant decline in the number of backward pushes (but not the jump clash) over fight duration, the decrease in bout duration and increase in retreats for fights that are decisively resolved indicate that this might be the case. This decline in rate of actions was not observed for inconclusively resolved fights suggesting that a minimum cost threshold must be reached before it becomes important in determining whether there will be a winner to a fight. These results support the idea that it is the rate at which damage is inflicted and accrued per unit time by competing individuals that is important in determining whether a fight is resolved decisively or whether it is inconclusive.

As indicated by an examination of the retreat over fight quarter, there was an increasing tendency for the retreat to be used as a fight progressed in fights that ended with a winner and loser. Therefore, as contest duration increased the likelihood of a decision to move away from an opponent being made also increased. Breaking physical contact and actively preventing further fighting by moving away from an opponent represents a low-cost (e.g., Hack, 1997; Rovero et al., 2000), low-risk strategy that is highly associated with losing a fight in this species (Jennings et al., 2002, 2003). The retreat was used as a strategy to break contact with an opponent and as such it appears to have a similar function to both the antler display (Jennings et al., 2002) and the parallel walk (Jennings et al., 2003). Our analysis indicated that the majority of retreats recorded were in the last quarter of fights that were decisively resolved consistent with the idea that the retreat is an indicator that one contestant, the loser, has reached its investment limit and determined that it cannot win the contest (Clutton-Brock et al., 1982).

The present study has established that fight structure differs depending on whether a contest concludes decisively or is inconclusive. Our evidence suggests that in order for a contestant to defeat his opponent he must engage in a significantly greater number of aggressive and presumably risky acts than his opponent does. This finding has wide support across a variety of species (e.g., Enquist et al., 1990; Popp et al., 1990; Turner, 1994; Briffa et al., 1998; Neat et al., 1998). If both opponents fail to establish a large enough difference in the rate of behavioural actions then a fight will end inconclusively, although studies on a variety of species have shown that in behaviourally matched contests a victor may eventually emerge (e.g., Marden & Waage, 1990; Smith et al., 1994; DiMarco & Hanlon, 1997). In addition, we have shown that the overall number of aggressive acts was significantly lower in fights that were inconclusive and that this is an important contributor to determining fight conclusion. We have also shown that fight duration and the total duration of bouts of fighting do not differ in the fallow deer based on fight conclusion. Therefore, the decision rule concerning how a contest is resolved is sensitive to differences in the magnitude of action performance between contestants and also, the rate of behavioural actions as a function of time spent fighting. This suggests an energetic explanation of fight conclusion based on the ability to incur and absorb costs of fighting (Payne & Pagel, 1996, 1997). The decision-making mechanisms employed by this species are poorly understood (Jennings et al., 2003), however, previous research has

suggested that fallow deer adopt a self-assessment rather than opponent assessment rule (Jennings et al., 2004, in press) and the results of the present study are consistent with this.

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